

APPENDIX L

MAXIMUM TEMPERATURE: UPPER OPTIMAL TEMPERATURE LIMITS FOR SALMONIDS IN THE WILLAMETTE AND LOWER COLUMBIA RIVERS

*Ann Richter and Steven Kolmes
Environmental Studies Program, University of Portland*

Introduction

The Willamette/Lower Columbia River Technical Recovery Team (WLC-TRT) is responsible for recommending delisting criteria. As these criteria need to address all the factors for species listing, they must make reference to habitat.

Adequate water quality is important to all salmonids at all life-history stages. The distributions of native salmonid fish in the Pacific Northwest are strongly tied to temperature conditions in their habitats. Because water temperature affects the health of individual fish, it also affects entire populations and species assemblages. Temperature may directly affect salmonids in obvious ways, or indirectly through interaction with other important variables (Dunham et al. 2001). For example:

- Given sufficient magnitude and time, high temperatures can cause weight loss, disease, competitive displacement by species better adapted to the prevailing temperature, or death (Sullivan et al. 2000).
- When fish are stressed by any one process, they are less able to deal with other stressors. Salmonids already stressed by high water temperature will be less able to deal with a second stressor (e.g., toxic pollutant, pathogen). Warmer temperatures often increase the infection rate or virulence of fish pathogens and lessen the ability of a fish to withstand disease (Materna 2001).

Human Influence on Thermal Regimes

In many streams that once were inhabited by large salmon runs, temperature regimes are now inhospitable. An important factor in the recovery of salmonid populations is the restoration of temperature regimes (Poole et al. 2001a, b).

Human activities can affect thermal regimes by simplifying the physical structure of aquatic systems, thereby eliminating natural thermal buffers and insulators (Poole and Berman 2001). Clearing and developing land, dredging or straightening streams, grazing and other land-

use activities influence temperature regimes by altering factors external to the stream, structures within the stream, and the amount of water flowing in the stream (Poole et al. 2001a, b). These activities often directly or indirectly simplify the structure of stream channels or riparian zones, as has occurred in the lower Willamette River (Sedell and Froggatt 1984). This type of channel simplification can potentially increase temporal variability and decrease fine-scale spatial variability in stream temperature, both of which may have negative consequences for salmonids (Poole et al. 2001b, Poole and Berman 2001). Removing riparian vegetation in small streams, where shading is important, can increase daily variation in stream temperature (Beschta 1997). For streams where groundwater buffers temperature, change in groundwater temperature or flow dynamics can alter the seasonal availability of cold water, including increased seasonal variation in water temperature. Small-scale thermal refugia can provide important habitat for salmonids during periods of warmer water temperatures (Ebersol 2002), but even slight changes in temperature extremes, or mean temperature, can result in refugium, and therefore salmonid, loss. Changes in the timing of maximum and minimum temperatures can occur with or without associated changes in the actual values of maximum, minimum, or mean stream temperatures, and these too can threaten salmonids because of their sensitivity to temperature at many life stages. Water temperature is an indicator of habitat quality, which is an integrator of what is happening in a watershed.

Thermal refugia are important in maintaining salmonid populations because when daily variation in stream temperature is high, salmonids may be exposed to stressful or lethal temperatures for part of the day. Thermal refugia provide protection for salmonids when temperatures are extreme (Ebersol 2002). At peak summertime temperatures, only a small percentage of habitat in some streams may be cool enough. Loss of riparian vegetation, the elimination of large beaver populations, removal of large woody debris, channel simplification, reduced groundwater discharge due to changes in upland vegetation, water withdrawals, and other human activities cause the loss of the fine-scale spatial distribution of appropriate thermal habitats upon which salmon rely (Poole et al. 2001b). This can cause fish to migrate greater distances to find appropriate habitats or not find them at all.

In the same way, seasonal variation in temperature can create thermal barriers to salmonid immigration and emigration. Anthropogenic activities can increase the coarse-scale temporal variation of streams, exposing salmonids to extremes beyond the normal range of variation and resulting in habitat fragmentation and elimination of the large, well-connected tracts of high-quality thermal habitat. This habitat fragmentation has been shown to degrade both population structure and persistence (Poole et al. 2001b).

In a recent draft document entitled Draft EPA Region 10 Guidance for State and Tribal Water Quality Standards,¹ the U.S. Environmental Protection Agency (EPA) recommended a four-part approach for state and tribal temperature standards to support native salmonids. This approach includes the adoption of:

1. thermal, potential numeric criteria for bodies of water, which are estimations (generally on the subbasin scale) of the thermal potential of bodies of water based on an average meteorological year, with adjustments for other climatic conditions;
2. interim, species-life-stage numeric criteria as a bridge until a newer approach to temperature criteria is developed;

¹ EPA. 2001. available at <http://yosemite.epa.gov/R10/WATER.NSF/1507773cf7ca99a7882569ed007349b5/ce95a3704aeb5715882568c400784499?OpenDocument>.

3. temperature management plan provisions; and
4. provisions to protect existing cold-water areas.

The EPA criteria are based on salmonid guilds. These guilds are described by the EPA as groups of species sharing similar life strategies, with similar temperature and habitat needs and limitations. In the Pacific Northwest, the cold-water guild includes the five Pacific salmon, anadromous steelhead trout, and coastal cutthroat and rainbow trout. This document discusses the species-specific data that exist, and then uses them as background criteria to support the EPA's recommended guild approach. The EPA draft criteria are being considered for application to potential salmonid habitat, as distinct from present or historical salmonid habitat. Potential habitat has not been explicitly identified by the EPA, but consists of those areas salmonids might inhabit without the dismantling of major barriers to passage. Whether the use of the potential habitat concept comes to closely match the spatial distribution and population number requirements eventually adopted by the National Marine Fisheries Service (NMFS) for delisting threatened or endangered salmonids, the guild approach associated with it can be evaluated separately in terms of maximum temperature criteria for salmonid delisting.

This paper will summarize the large body of information about thermal effects on salmonids, specific to life stage and species, and use that information to propose draft water temperature criteria. Several groups that recently produced white papers on the topic are the Pacific Northwest Environmental Indicator Work Group (PNWEIWG), the Sustainable Ecosystems Institute (SEI), the EPA Water Temperature Criteria Technical Workgroup, the Columbia River Inter-Tribal Fish Commission, and the Washington State Department of Ecology. The participating agencies in the PNWEIWG are the British Columbia Ministry of Environment, Lands, and Parks; the Alaska Department of Environmental Conservation; the Idaho Division of Environmental Quality; the Washington State Department of Ecology (WDOE); Environment Canada; and the U.S. EPA (Region 10). In 1997, directors of these agencies asked the PNWEIWG to pilot development of regional indicators associated with risks to salmonid stocks. Indicators were required to: (1) have data available, (2) be integral to measuring the performance of salmon issues for PNWEIWG agencies, and (3) be able to be reported cost-effectively in a monitoring program.

Martin Environmental, Parametrix Inc., and Weyerhaeuser Company participated in the SEI, which was funded by the Oregon Forest Industries Council, Washington Forest Protection Association, and Weyerhaeuser Company. The SEI developed a risk-based approach to analyze summer temperature effects on juvenile salmon species in their December 2000 publication, *An Analysis of the Effects of Temperature on Salmonids of the Pacific Northwest with Implications for Selecting Temperature Criteria* (Sullivan et al. 2000). This report reviewed the aspects of temperature affecting the rearing of salmonid species in the freshwater environment and discussed lethal (acute) as well as sublethal (chronic) effects. The main focus of the report was on temperatures affecting growth and mortality (Sullivan et al. 2000).

The EPA established the Water Temperature Criteria Technical Workgroup to assist in developing temperature criteria guidance for EPA Region 10. The purpose of the EPA guidance is to help Pacific Northwest states and tribes adopt water temperature standards that (1) meet the biological requirements of native salmonid species (Pacific salmon, trout, and charr) for survival and recovery pursuant to the Endangered Species Act (ESA); (2) provide for the protection and propagation of salmonids under the Clean Water Act (CWA); and (3) meet the salmonid restoration goals of federal trust responsibilities with treaty tribes. The technical workgroup, a

panel of experts on salmonid biology and stream temperature, represented the following agencies: EPA, U.S. Forest Service, WDOE, NMFS, U.S. Fish and Wildlife Service, Columbia River Inter-Tribal Fisheries Commission, Idaho Department of Environmental Quality, Oregon Department of Environmental Quality, U.S. Geological Survey (USGS) Biological Resources Division, and USGS Water Resources Division. In 2001, the technical workgroup submitted a final summary report to the policy workgroup of the EPA Region 10 Water Temperature Guidance Project entitled *Technical Synthesis: Scientific Issues Relating to Temperature Criteria for Salmon, Trout, and Charr Native to the Pacific Northwest*.² Five technical summaries on the major physical and biological considerations for developing water temperature standards were developed to provide a scientific foundation for the project:

1. thermal effects on salmonid physiology (McCullough et al. 2001),
2. thermal effects on salmonid behavior (Sauter et al. 2001),
3. interactions between multiple stressors—thermal and other—affecting salmonids (Materna 2001),
4. thermal influences on salmonid distribution (Dunham et al. 2001), and
5. spatial and temporal variation in patterns of stream temperature (Poole et al. 2001a, b).

McCullough (1999) of the Columbia River Inter-Tribal Fish Commission, prepared a summary report for EPA Region 10, in which he reported that significant impacts to survival due to temperature regime can occur in all life stages. Sublethal impacts to life processes such as growth, survival, reproductive success, migration success, disease, feeding, territoriality, aggressiveness, swimming, and bioenergetics can cumulatively result in diminished survival and production of the population.

In December 2000, the WDOE Water Quality Program released a draft discussion paper and literature summary addressing temperature criteria that included recommendations for chinook, coho, and chum salmon and steelhead at critical life stages (WDOE 1999). The recommendations were based on a thorough review of the literature and laboratory data adjusted for application to natural waters.

The following sections discuss the scientific findings on the thermal effects and requirements of salmonids, in general and by individual species, and attempt to draw together materials from the documents listed above.

General Salmonid Data

Smoltification

High temperatures during the smolt phase can result in outright lethality, premature smolting, blockage of seaward migration, desmoltification, shifts in emigration timing resulting in decreased survival in the marine environment, and other stresses detrimental to fitness.

² Available in final form at

<http://yosemite.epa.gov/R10/WATER.NSF/6cb1a1df2c49e4968825688200712cb7/bd029c92a81bf25f88256a020072a8c7?OpenDocument>.

Temperatures that have been reported for impairing smoltification are above a range from approximately 12° to 15°C or more (McCullough et al. 2001).

Adult Migration

Thermal blockages to adult salmon migration have also been identified. Migration blockages occur consistently in the temperature range of 19° to 23°C (McCullough et al. 2001). For chinook and sockeye salmon and steelhead in the Columbia River 21.7° to 23.9°C has been cited as the temperature range blocking migration (Fish and Hanavan 1948).

Spawning

Elevated temperatures can cause migration delays in salmonids that alter timing of key processes, such as spawning, or can lead to stress, disease, bioenergetic depletion, or death. If salmonids such as fall chinook or coho are exposed to high temperatures just before or during spawning, gametes held internally in adults can be severely affected, resulting in a loss of viability that appears as poor fertilization rate or embryo survival. McCullough et al. (2001) concluded that egg mortality, alevin development, and egg maturation are negatively affected by exposure to temperatures above approximately 12.5° to 14°C. A spawning temperature range of 5.6° to 12.8°C (maximum) appears to be a reasonable recommendation for Pacific salmon, unless colder thermal regimes are natural in any tributary (McCullough et al. 2001).

Lethality

Analysis of lethal temperature suggested that a threshold of 26°C for annual maximum temperature is a signal of imminent risk of direct mortality (Sullivan et al. 2000). A site-specific analysis of duration of exposure when annual maximum temperature is between 24°C and 26°C is also recommended to ensure that duration/magnitude thresholds are not exceeded. These annual maximum temperature values are intended to apply to all salmon and trout species in natural rivers and streams in the Pacific Northwest (Sullivan et al. 2000).

Distribution

After a review of field studies for chinook salmon, steelhead, and rainbow trout, McCullough (1999) showed that the distributional limit of these salmonids corresponds approximately to a mean daily water temperature of 20°C and a maximum daily water temperature of 22° to 24°C. Hokanson et al. (1997) showed that water temperatures greater than 23°C, even for short periods (hours), result in Pacific salmon and trout moving into cold-water refugia. Eaton et al. (1995) proposed a higher (95th percentile) weekly mean temperature tolerance for chinook (24°C) and coho (23.4°C) salmon, when the fish temperature database matching system (FTDMS) approach was used to evaluate various distribution records for 30 common North American fish species. However, when using the FTDMS approach, the existence of thermal refugia provides a potential source of error (Eaton 1995), and leads to recommendations inconsistent with other studies. Many important salmon diseases become

virulent above 15.6°C, which makes the impact to population production potentially more severe, because as temperatures rise toward the limits to salmonid growth, the mortality rate increases. The balance may shift to zero net growth, even at lower temperatures. In general, juvenile salmonids appear to have final temperature preferences in the range 11.7° to 14.7°C (Ferguson 1958, Countant 1977, Jobling 1981, McCullough, 1999).

From a behavioral perspective, Sauter et al. (2001) suggest that water temperature affects some aspects of juvenile life-history patterns, including duration of freshwater rearing and outmigration timing. Elevated water temperatures inhibit gill ATPase activity, an enzyme that prepares juvenile salmonids for osmoregulation in seawater during emigration. Decreased gill ATPase activity is associated with loss of migratory behavior in anadromous juvenile salmonids. Spring water temperatures must not exceed 12°C for successful smoltification in steelhead. For spring chinook and coho this value is 15°C, and it may be higher for summer migrating fall chinook subyearlings (Zaugg and Wagner 1973). In addition, higher water temperatures and longer exposure to warm water increase the feeding rate of predatory species consuming juvenile salmonids. Interspecific competition also appears to play a role in the distribution and thermal preferences of juvenile salmonids (Sauter et al. 2001).

Swimming Speed

If water temperature is too high, changes in swimming speed can impair adult migration. Fish may refuse to migrate, migrate back downstream, or seek shelter in tributaries or other available cold-water refugia. Swimming speed is also vital to smolts' ability to maintain position in the current, control rate of descent, and avoid obstacles. In addition, high temperature can impair their ability to swim in quick bursts, which is necessary to avoid predators (McCullough et al. 2001).

Chemical Constituents

Many chemical constituents are affected by temperature. Most notably, dissolved oxygen (DO) decreases with increasing temperature. When fish experience temperature stress, they may also experience stress from low DO levels. McCullough (1999) showed that adult migration of chinook salmon can be impeded when temperature and DO requirements are not met. It is also well documented that the concentration of ammonia increases with increasing temperature (EPA 1985). Although there is no single pattern that explains the effects of temperature on the toxicity of pollutants to aquatic organisms, some evidence shows that temperature may change the rate of toxification under chronic exposures (Mayer et al. 1994). Since rising temperatures result in an increase in metabolic processes, gill ventilation must also rise proportionately (Heath and Hughes 1973). Black et al. (1991) showed that an increase in water flow over the gills, which may result from increased gill ventilation at increased temperature, resulted in rapid uptake of toxicants via the gills. Sublethal exposure to toxicants can reduce the upper lethal temperatures of fish, constricting the thermal tolerance zone (Paladino et al. 1980), and fish that are weakened by other causes may be much more sensitive to toxic chemicals (Jobling 1994). Temperature has been found to significantly increase the toxicity of some organic chemicals such as terbufors, trichlorfon, and 2,4 dinitrophenol (Howe et al. 1994), as well as some metals such as mercury

(MacLeod and Pessah 1973, Materna 2001). There is evidence that higher temperatures can help fish to withstand ammonia (cited in Sullivan et al. 2000).

Disease

Most fish diseases are exacerbated by higher water temperatures (Ordal and Pacha 1963) and can infect salmon at many life stages. Diseases associated with warm water in the Pacific Northwest are well documented. They include the bacterial infections *columnaris*, caused by *Flexibacter columnaris*; bacterial kidney disease (BKD), caused by *Renibacterium salmoninarum*; the bacterial pathogens *Aeromonas salmonicida*, *A. punctata*, *A. hydrophila*; and the protozoan parasite *Ceratomyxa shasta*. Evidence from Idler and Clemens (1959), Williams et al. (1977), Bouck et al. (1970) (as cited by EPA and NMFS 1971), and Ordal and Pacha (1963) indicates that temperatures of 16.7° to 20°C or higher, lead to infection of adult salmon with *columnaris*, even with exposure to low-virulence strains, and infection can occur at even lower temperatures with high-virulence strains. Evidence from Colgrove and Wood (1966) indicates that temperatures between 13.9° and 15.6°C constitute a transitional temperature region below which recovery from *columnaris* after infection could occur, and above which infection and mortality increase. Laboratory and field studies by numerous investigators show that infection and mortality by *columnaris* disease were negligible at temperatures $\leq 12.8^\circ\text{C}$, but temperatures $\geq 15^\circ\text{C}$ produced significantly increased mortalities. Not only do juvenile survival rates decrease with increasing temperature, but Fryer and Pilcher (1974) also showed that time to death decreases with increasing temperature for juvenile chinook salmon, coho salmon, and steelhead (Materna 2001).

BKD is also a prevalent disease in which temperature has been shown to have an effect on the mortality of infected salmonids. In an experiment involving infected sockeye, coho, and steelhead over a range of temperatures from 4° to 20.5°C, the highest mortalities due to BKD occurred at 12.2°C, with declining mortalities at higher or lower temperatures (Fryer and Sanders 1981, as cited in Chapman et al. 1991). It is important to remember that elevated temperatures do not increase mortality from all salmonid diseases; in fact, some diseases have higher mortalities at temperatures well within an otherwise optimal range.

Groberg et al. (1978) studied the relationship of water temperature to infections of coho salmon, chinook salmon, and steelhead with *A. salmonicida* and *A. hydrophila*. Among the three salmonid species, at 3.9° and 6.7°C, mortality in fish infected with *A. salmonicida* varied from 2 to 26%; at 20.5°C, 93 to 100% died within 2 or 3 days; at 6.7°C or lower survival was 12 to 23 days. Results from experiments with *A. hydrophila* gave similar results. At 20.5°C, mortality ranged from 64 to 100%; at 9.4°C or below, no deaths occurred.

General Recommendations for Salmonids

The Pacific Northwest Salmon Habitat Indicators Work Group (PNWSHIWG). (1998) identified maximum water temperature as an influence on salmonid migration patterns, development of eggs to alevins, fry emergence, metabolism, behavior, susceptibility to parasites and disease, and mortality. Water exceeding 20°C was categorized as causing “severe impairment.”

Chinook Salmon Data

Incubation and Early Fry Development

Based on the works of Donaldson (1955), Garling and Masterson (1985), Seymour (1956), Eddy (1972, as cited in Raleigh et al. 1986), Burrows (1963), Baily and Evans (1971), Heming (1982), Heming et al. (1982), the following temperatures are strongly suggested to provide optimum conditions for incubation and early fry development for chinook salmon. Constant temperatures above 9° to 10°C may reduce the survival of embryos and alevins. Temperatures of 11° to 12°C can still result in good survival, however the results are consistently less than what is produced at lower temperatures (McCullough et al. 2001). Incubation temperatures from 13.9° to 19.4°C have been associated with complete mortality while significant mortality (over 50%) has been noted at constant incubation temperatures from 9.9° to 16.7°C (Hicks 2000).

Juvenile Rearing and Growth

Optimal rearing temperatures at natural feeding regimes are in the range of 12.2° to 14.8°C for chinook salmon (Hicks 2000). Banks et al. (1971, as cited by Garling and Masterson 1985), Clarke and Shelbourn (1985), Brett et al. (1982), and Marine (1997) reported optimum growth temperatures determined from feeding on full rations that range from 14.8° to 20°C. Ration size in the laboratory and food supply in nature can have significant effects on optimal temperatures for rearing, and this complication is one that must be kept in mind when evaluating temperature effects in eventual monitoring and evaluation efforts. Feeding rates below the satiation level typical of field situations are associated with reduced optimum growth temperatures (Elliott 1981). Brett et al. (1982) reported an optimal growth temperature of 19°C for chinook maintained in the laboratory at maximal daily ration, but that growth rates in the field corresponded to a projected feeding level of 60% of maximal daily ration, which translated to an optimal growth temperature of 14.8°C for the field population.

Smoltification

Although data on temperature impairment of smoltification is incomplete, the existing literature suggests that temperatures should be generally maintained below 12° to 13.8°C during outmigration of chinook salmon smolts (Hicks 2000). The temperature threshold for impairment of smoltification was found to be 12°C by Zaugg (1981) in spring chinook yearlings, while Marine (1997) found it to occur at 17° to 20°C in fall chinook subyearlings.

Adult migration

Immigrating spring chinook salmon in the Willamette River have experienced thermal blockages at 21° to 22°C (at oxygen 3.5 mg/l) (Alabaster 1988). A temperature of 21°C blocked migration of spring chinook salmon in Clearwater, Idaho, (Stabler 1981) as well as summer chinook salmon (Stuehrenberg et al. 1978, as cited by Dauble and Mueller 1993) of the Snake

River. A temperature of 21.1°C blocked spring chinook in the Tucannon River (Bumgarner et al. 1997), and fall chinook in the Sacramento River were blocked at 19° to 21°C (oxygen ~ 5mg/l) (Hallock et al. 1970).

Spawning

The following authors reported spawning temperature ranges in daily average temperatures (DAT) for chinook salmon. For spring chinook salmon, Olson and Foster (1955) reported 4.4° to 17.8°C. For fall/summer chinook, Raleigh et al. (1996, cited in ODEQ 1995) reported 5° to 13.4°C. The majority of the temperature observations reviewed in Hicks (2000) cited a maximum spawning temperature below 14.5°C for chinook salmon.

Lethality

For chinook salmon, the upper incipient lethal temperature (UILT) has been recorded at 25.1°C (acclimation temperature 20° and 24°C) by Brett (1952), and 24.9°C (acclimation temperature 21.1°C) by Orsi (1971).

Behavior

For subyearling spring chinook salmon in the Dungeness River, Brett (1952) found the acute preference temperature to be 12° to 13°C at all acclimation temperatures and the mean final preference temperature was 11.7°C. Sauter (1996) found that spring chinook salmon smolts on unlimited ration have a final temperature preference of 16.7°C and Spigarelli (1975) reported that adults prefer a field temperature of 17.3°C. For fall chinook salmon, Sauter (1996) found parr to prefer a mean 16.7°C, while advanced smolts preferred 10.9°C.

Recommendations for Chinook Salmon

Incubation and Early Fry Development

McCullough et al. (2001) recommended that temperatures be maintained below 12°C for incubation and fry development, and Hicks (2000) recommended an adjusted 7-day average of the daily maximum temperatures (7-DAM) of 11° to 12°C at the time of fertilization of chinook salmon eggs. Both McCullough et al. (2001) and Hicks (2000) recommended and that individual daily maximum temperatures (1-DM) of 13.5° to 14.5°C are required to provide optimal protection from fertilization through early fry development.

Growth

McCullough (1999) suggested using the growth optimum of 15.6°C for spring chinook salmon as the temperature standard, because temperatures lower than this cause no reduction in survival while temperatures higher than this begin to reduce growth and lead to increasing

mortality rates. A synthesis of evidence from Bisson and Davis (1976) (as cited by Garling and Masterson 1985), Brett et al. (1982), Marine and Cech (1998), Wilson et al. (1987), Reiser and Bjornn (1979), and Brett (1952), lead McCullough et al. (2001) to recommend an optimum production temperature zone of 10.0° to 15.6°C. Adjusting laboratory temperatures to naturally fluctuating stream temperatures, Hicks (2000) recommended that a 7-DAM of 14.2° to 16.8°C during the peak of summer provides for optimal growth conditions for chinook salmon.

Adult Migration

Hicks (2000) recommended that daily maximum temperatures should not exceed 20° to 21°C in order to prevent migration blockage of adult chinook salmon.

Lethality

Hicks (2000) recommended that to protect fish from acute lethality, daily maximum temperatures not exceed 22°C. In addition, he recommended that thermal plumes should not be allowed such that fish could become even briefly exposed to water warmer than 30° to 32°C.

Coho Salmon Data

Incubation and Early Fry Development

From the studies of Dong (1981), Tang et al. (1987), Murray -and McPhail (1988), Velsen (1987), and Davidson and Hutchinson (1938) (as cited in Sandercock 1991), it is relatively clear that egg survival for coho salmon is consistently best at constant temperatures of 2.5° to 6.5°C, but may still be acceptable for many stocks at temperatures of 1.3° to 10.9°C. Alevin and fry survival and health may be best at constant temperatures of 4° to 8°C, but survival may remain acceptable up to 10.9°C. A constant 12°C may form the upper threshold for optimal development of coho salmon eggs and alevin (McCullough et al. 2001, Hicks 2000).

Flett et al. (1996) investigated the cause of low survival to hatch of embryos (42%) of coho salmon from the Fairview, Pennsylvania, stock in Lake Erie in 1988. It was proposed that the low survival was due to delayed oocyte maturation, ovulation, and vent maturation. Flett et al. (1996) suggested this was caused by exposure of the salmon to warm water (above 20°C in his Fairview stock and 2° to 4°C higher than in the Simcoe stock, which showed no such impairments) during late ovarian maturation and migration.

Juvenile Rearing and Growth

Most literature shows that juvenile coho salmon are not particularly sensitive to stream temperatures and generally suggests maximum temperatures between 9.4° and 14.4°C as optimal. However, Everson (1973, as cited by Sullivan et al. 2000) found that, depending on food availability, growth optima occur at 15°C. Average or constant temperatures of 12° to 15°C probably best characterize optimal rearing conditions (Hicks 2000). The Sustainable Ecosystems Institute review (Sullivan et al. 2000) suggested 12° to 17°C as an acceptable temperature range.

Smoltification

Both Zaugg and McLain (1976) and Adams et al. (1975) reported the temperature threshold for impairment of smoltification of coho salmon to be 15°C.

Spawning

It has been reported that spawning activity in coho salmon may typically occur in the range of 4.4° to 13.3°C (Hicks 2000), although Bell (1973) suggested that temperatures should be within the range of 7.2° and 15.6°C for successful spawning of coho salmon. Bell (1991) reported a DAT of 10° to 12.8°C for spawning coho salmon.

Lethality

For coho fry, Brett (1952) reported UILT (the temperature at which 50% of the population is dead after indefinite exposure) at 25.0°C (acclimation temperatures of 20° and 23°C). Konecki et al. (1995) tested juvenile coho salmon fry critical thermal maximum (CTM, the species-specific temperature at which a fish loses equilibrium and dies, which depends on acclimation temperature). Mean CTMs from three populations captured in the field in Washington State were 28.2°, 29.1°, and 29.2°C, which exceed published data from some laboratory tests for juvenile coho (Beschta et al. 1987, DeHart 1975, McGeer et al. 1991). The population from a relatively cool stream had a lower CTM than two populations from warmer streams. After three months in the laboratory under constant temperature regimes the CTMs no longer differed. This indicated that the population-specific differences resulted from different acclimation regimes rather than from genetic adaptation. Constant exposure to temperatures of 22° to 23°C poses a risk of causing direct lethality to juvenile coho salmon (Hicks 2000).

Behavior

For subyearling coho salmon, Brett (1952) reported a range of 12° to 14°C for their temperature preference, which is affected by acclimation temperature. Konecki et al. (1995) reported 11.6°C (range 7° to 21°C) and 9.9°C (range 6° to 16°C) for the final temperature preference (species-specific value that may be influenced by feeding level) for subyearling coho salmon in two different creeks. Reutter and Herdendorf (1974) reported that adult coho have a final preference temperature of 11.4°C, while Spigarelli (1975) reported a preferred field temperature of 17.3°C.

Swimming Speed

Brett et al. (1958) investigated the effect of temperature on the cruising speed of young coho salmon. Cruising speeds of subyearling and yearling coho were determined for acclimation temperatures ranging from 1° to 24°C. Optimum cruising speed for juvenile coho occurred at 15°C.

Disease

Groberg et al. (1983) studied the effects of water temperature on infection by the predominantly marine pathogen *Vibrio anguillarum* in juvenile coho salmon at seven water temperatures range from 3° to 21°C. More rapid death and higher mortality were observed at the elevated water temperatures. Growth rates of *V. anguillarum* were directly related to temperature.

Recommendations for Coho Salmon

Incubation and Early Fry Development

Adjusting laboratory temperatures to naturally fluctuating stream environments resulted in a recommendation of a 7-DAM of 9° to 12°C to fully support the pre-emergent states of coho salmon (McCullough et al. 2001, Hicks 2000).

Juvenile Rearing and Growth

Adjusting for a naturally fluctuating stream environment resulted in a recommendation of 14° to 17°C for the 7-DAM to fully protect juvenile coho salmon rearing (Hicks 2000).

Sullivan et al. (2000) developed and used a bioenergetics-based approach to evaluate salmon growth in relation to environmental temperature, and to suggest sublethal temperature thresholds for coho salmon. An upper threshold for the 7-DAM temperature of 16.5°C was found to be appropriate, assuming a 10% reduction in growth represents an appropriate risk level (Sullivan et al. 2000).

Lethality

Subtracting a 2°C safety factor resulted in a recommendation of 20° to 21°C to avoid direct lethality to coho salmon (Hicks 2000).

Chum Salmon Data

Incubation and Early Fry Development

Based on the works of Murray and Beacham (1986), Beacham and Murray (1985), and Zinichev and Zotin (1988), constant incubation temperatures from 4° to 12°C commonly produce excellent incubation results for chum salmon; however, some researchers have noted that less-than-optimal survival occurs at the edges of this range. Both McCullough et al. (2001) and Hicks (2000) suggested that constant initial incubation temperatures of 8° to 10°C would be most consistently optimal for chum salmon.

Juvenile Rearing

Optimal rearing occurs between about 13° to 14.5°C (Hicks 2000).

Spawning

The Independent Scientific Group (1996) reported an average range of 8° to 13°C for spawning, while Hicks (2000) reported that chum salmon most consistently spawn within a range of 7° to 10.5°C.

Lethality

Brett (1952) reported the UILT for chum salmon fry at 23.7° and 23.8°C (acclimation temperature 20° and 23°C, respectively). Hicks (2000) stated that significant lethality to chum salmon can result from constant exposure to 22° to 23°C.

Behavior

Brett (1952) reported that juvenile subyearling chum salmon have an acute preference temperature of 12° to 14°C at all acclimation temperatures and final preference temperature of 14.1°C. Groot and Margolis (1991) reported adult migrant chum have an acute preference temperature of 7° to 11°C.

Recommendations for Chum Salmon

Incubation and Early Fry Emergence

Hicks (2000) recommended that the 7-DAM should not exceed 10° to 12°C for fertilization through fry emergence.

Lethality

With the 2°C safety factor, it was recommended that daily maximum temperatures should not exceed 20° to 21°C to prevent direct lethality to chum salmon. In addition, fish should not be exposed even briefly to temperatures greater than 33° to 34°C (Hicks 2000).

Steelhead Data

Incubation and early fry development

Considering the works of Fuss (1998), Bell (1986), Rombough (1988), and Redding and Schreck (1979), it appears that an optimal constant incubation temperature occurs below 11° to 12°C for steelhead (McCullough et al. 2001).

Juvenile Growth

Optimal growth for juvenile steelhead occurs in the range of 14° to 15°C (Hicks 2000); although in a laboratory setting, Wurtsbaugh and Davis (1977) found that steelhead growth could be enhanced by temperature increases up to 16.5°C.

Smoltification

For steelhead, Hoar (1988) reported temperatures higher than 13°C, Adams et al. (1975) reported higher than 12.7°C, Zaugg et al. (1972, as cited by Zaugg and Wagner 1973) reported higher than 13.6°C and Zaugg (1981) reported 12°C as upper thresholds for impairment of smoltification.

Adult migration

Strickland (1967, as cited by Stabler 1981) reported 21°C as the temperature blocking adult steelhead migration in the Snake River.

Spawning

For steelhead, Bell (1991) reported a daily average temperature range of 10° to 12.8°C for spawning.

Behavior

For subyearling steelhead in the South Umpqua River, with food available, the preferred temperature was 15.0°C and 17.8°C for yearlings (Roper and Scarnecchia, 1994).

Nielsen et al. (1994) studied steelhead use of thermally stratified pools in Northern California streams. It was observed that 65% of the juvenile steelhead in Rancheria Creek moved into thermal refugia—in the form of adjacent stratified pools—during periods of high ambient stream temperatures of 23° to 28°C. Just before moving into these pools, fish showed a decline in foraging behavior and increased agonistic activity. On the Middle Fork Eel River, summer-run steelhead adults were found in deep stratified pools throughout the summer, when midday ambient stream temperatures ranged from 26° to 29°C; these cold water pockets were on average

3.5°C cooler than the stream. Where stream temperatures reached upper incipient lethal levels, these thermally stratified pools provided refuge habitat for significant numbers of young-of-the-year, yearling, and adult steelhead.

Recommendations for Steelhead

Incubation and Early Fry Development

Based on the literature and adjusting for a naturally fluctuating river environment, the recommendation of 13.5° to 14.5°C for the single daily maximum temperature from fertilization through hatching was made by Hicks (2000).

Juvenile Rearing and Growth

The adjusted value for recommendation to fully protect juvenile rearing of steelhead was 16° to 17°C (Hicks 2000). Sullivan et al. (2000) recommended the upper threshold for the 7-DAM temperature of 20.5°C for steelhead, assuming that a 10% reduction in growth is an acceptable risk level.

Smoltification

Hicks (2000) adjusted constant temperature ranges to the fluctuating stream environment, and recommended a 7-DAM of 13.3° to 14.3°C for emigrating steelhead smolts.

Adult Migration

Based on the consistency of several studies, Hicks (2000) recommended that temperatures remain lower than 21° to 22°C (1-DAM) to prevent thermal barriers to migrating steelhead, and that water in which steelhead migrate or hold not exceed a 7-DAM of 16° to 17°C.

Lethality

Hicks (2000) recommended that daily maximum temperatures remain below 19° to 20°C to prevent directly lethal conditions to steelhead.

Draft Criteria

The EPA (2001) recommends that temperature-limit criteria be based upon upper optimal physiological temperature preferences known to support requisite biological processes of recognized salmonid life-history stages. Moreover, the EPA (2001) recommends that the criteria be based on guilds of salmonids, taking the spatio-temporal use of the landscape by guild members into account. For the Lower Columbia and Willamette Rivers, the guild present is the cold-water guild. Along with the population growth and abundance criteria being developed by

the WLC-TRT and reported elsewhere, we suggest that temperature-based criteria for the delisting of threatened and endangered salmonids under the Endangered Species Act, written to be consistent with EPA upper optimal temperature values, consist of two parts:

1. A requirement that in order to delist salmonids in the Willamette and Lower Columbia River domain, the 7-DAM temperature maxima within the habitat of a given evolutionarily significant unit (ESU) must not be increasing over the course of 20 years. This requirement of thermal nondeterioration is intended to complement requirements for nondeterioration in population growth rates and abundance. Prior to delisting, data will need to be collected to show with high confidence that the slope of the observed temperature trend is less than or equal to zero. The 20-year period provides a long enough data set to avoid being confounded by temperature oscillations driven by the Pacific Decadal Oscillation (PDO) (Anderson 1998, Chao et al. 2000), which has considerable effects on climate in the Pacific Northwest.
2. Upper optimal temperature criteria be adopted, above which delisting cannot occur regardless of whether or not the direction of change is nondeteriorating. We suggest the following as temperature maxima above which delisting cannot occur for chinook, coho, chum salmon, and steelhead:

	7-Day-Average Maximum Daily Temperatures	Weekly Mean Temperatures
Spawning and incubation	13°C (55°F)	10°C (50°F)
Juvenile rearing	16°C (61°F)	15°C (59°F)
Adult migration	18°C (64°F)	16°C (61°F)
Smoltification except steelhead	16°C (61°F)	15°C (59°F)
Steelhead smoltification at fourth-level HUC ^a watershed	14°C (57°F)	12°C (54°F)

^a HUC = hydrologic unit code

For all these criteria, the significant challenge of defining the spatiotemporal range over which they should be applied remains. Those spaces occupied by threatened and endangered salmonids need to be regulated at the times of year that sensitive life stages are present, and defining the bodies of water involved and the times to apply the standards requires additional consideration and research. The concept of assessing thermal potential being developed by the EPA involves modeling the characteristics of bodies of water in order to determine whether a distribution of temperatures sufficient to support salmonids (and other beneficial uses) can be attained (see “Public Review Draft” at <http://www.tboys.com/chalk2.htm>). Using this use-attainability analysis, as prescribed by the existing Clean Water Act, there is no obligation to provide unattainable conditions (in this case to apply the temperature criteria). It may be that as the EPA develops concepts related to use-attainability analysis (including appropriate model selection, sensitivity analysis, and determination of an acceptable level of anthropogenic degradation), it will begin to converge with the efforts of the WLC-TRT and others involved in salmon recovery planning to define spatio-temporal ranges over which maximum temperature criteria will be applied. Some amelioration of the difficulties posed by this challenge may be provided by the multiple runs and species that broaden the times of concern beyond brief periods

for many subbasins. Once the spatio-temporal pattern to apply these standards has been defined for any ESU, exemptions to the above temperature maxima for specific bodies of water can still be proposed based on historical acclimation to higher temperatures. Such an exemption would require physiological or population-level evidence that higher temperature maxima would not harm the fish native to that area, or that cold-water refugia are plentiful and provide the circumstances required for salmonid survival. Evidence required for an exemption would need to include the density, size, and duration of thermal refugia; data indicating that the distribution of refugia in space and time is adequate to be protective of the salmonids (Ebersol 2002); and field and laboratory studies providing strong evidence of physiological acclimation for the existing local population whose habitat is under consideration.

The guild-based temperature criteria are supported by the data collected for the salmonid species at the Willamette and Lower Columbia Rivers. The relationships between individual species data and the guild-based criteria are described briefly in the following paragraphs.

Spawning and Incubation

The 10°C weekly mean temperature criterion is consistent with the upper temperature range for optimum survival of chinook salmon embryos and alevins (Raleigh et al. 1986) and is within reported temperature ranges for successful spawning (Olson and Foster 1955, Raleigh et al. 1986), although the majority of spawning observations reported by Hicks (2000) recommended maximum temperature values for chinook salmon consistent with the proposed criterion of 13°C.

For coho salmon, the weekly mean temperature criterion of 10°C is at the upper end of their acceptable incubation temperature range (McCullough et al. 2001, Hicks 2000). This criterion is within the acceptable range of coho spawning temperatures (Hicks 2000, Bell 1973).

For chum salmon, the 10°C weekly mean temperature criterion is within their safe temperature range for spawning (Hicks 2000) and incubation (McCullough et al. 2001, Hicks 2000).

Steelhead spawning occurs at temperatures within the range protected by the 10°C (weekly mean temperature criterion), as does their early fry development (McCullough et al. 2001).

Juvenile Rearing

The 15°C weekly mean temperature criterion is at the upper edge of optimal rearing temperatures for chinook with a natural feeding regime (Hicks 2000).

The 15°C weekly mean temperature criterion is at the upper end of the temperature range providing optimal rearing conditions for coho salmon (Hicks 2000).

The 15°C weekly mean temperature criterion is slightly above the optimal range for chum rearing reported by Hicks (2000).

Optimal growth temperatures for juvenile steelhead are in the range of 14° to 15°C (Hicks 2000), although in a laboratory setting slightly higher temperatures were associated with a food supply in excess of that characteristically available in nature (Wurtsbaugh and Davis 1977).

Smoltification

The extreme variability of habitat use by steelhead makes establishing a temperature criterion for their smoltification challenging. The 12°C proposed for a weekly mean temperature at the fourth-level hydrologic unit (HUC) watershed is consistent with Zaugg and Wagner's (1973) gill ATPase activity data. Weekly mean temperature values of 15°C proposed as criteria for other salmonids are well above the values having excessive physiological consequences for steelhead (Zaugg and Wagner 1973). The results of Adams et al. (1975) and Hoar (1988) support this lower criterion for steelhead.

The weekly mean temperature criterion of 15°C may be more protective of fall chinook salmon (Marine 1997) than spring chinook (Zaugg 1981). Hicks (2000) found that temperatures above 13.8°C did produce smoltification impairment in chinook.

For coho salmon the 15°C weekly mean temperature criterion is at the threshold temperatures that cause smoltification impairment.

Adult Migration

The proposed maximum temperature criterion of 16°C is within the safe range proposed for chinook temperature maxima by Hicks (2000) and seems protective for coho and chum salmon survival during adult migration as well (Hicks 2000). Adult migrant chum have a somewhat lower temperature preference of 7° to 11°C (Groot and Margolis 1991). Adult steelhead migration is not blocked until 21°C (Strickland 1967, as cited by Stabler 1981). Steelhead have been reported to make use of deep stratified pools as thermal refugia when midday ambient stream levels ranged above their tolerance limits (Nielsen et al. 1994).

Framework for Temperature Criteria

Salmonid survival and recovery will require more than the attainment of these temperature goals. A rich data set shows that in terms of thermal tolerances, disease resistance and physiological adaptation in general salmonid stocks native to specific bodies of water may be better adapted to local conditions than are other members of their species. However, in many populations the genetic modification due to hatchery operations may significantly reduce the present levels of local adaptation. Definitive criteria for salmonid recovery should eventually define ways to incorporate spatio-temporal variability into them in a realistically complex fashion and have as their eventual goal a process that realigns the curves of current environmental variables so that they overlay historic conditions rather than simply acting as a floor or ceiling. The challenge of this task is exacerbated by the multiple salmonid life stages that will need to be identified in their distribution over space and time and monitored. It is crucial that along with the attainment of habitat goals, historical salmonid populations be identified and recovered in a way that maintains them in the milieu suitable for their survival. Hatchery operations may need to be adjusted to serve this goal. Salmonid harvest patterns and hydro operation management may both need to take the significance of both environmental recovery and the relationships of specific genetic stocks to their native rivers into account (this study

provides no information on hatcheries, hydro, or harvest). The complexity of any solution to the problem of salmonid survival will need to balance all of these considerations while achieving temperature regimes suitable for the persistence of the salmon ESUs.

Literature Cited

- Adams, B. L., W. S. Zaugg, and L. R. McLain. 1975. Inhibition of salt water survival and Na-K-ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperatures. Trans. Am. Fish. Soc. 104(4): 766–769.
- Alabaster, J. S. 1988. The dissolved oxygen requirements of upstream migrant chinook salmon, *Oncorhynchus tshawytscha*, in the lower Willamette River, Oregon. J. Fish Biol. 32: 635–636.
- Anderson, J. 1998. Decadal climate cycles and declining Columbia River salmon. Sustainable fisheries conference proceedings, 22 p.
Available at <http://www.cqs.washington.edu/papers/jim/victoria.html>.
- Bailey, J. E., and D. R. Evans. 1971. The low-temperature threshold for pink salmon eggs in relation to a proposed hydroelectric installation. Fish. Bull. 69: 587–593.
- Beacham, T. D., and C. B. Murray. 1985. Effect of female size, egg size, and water temperature on development biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. Can. J. Fish. Aquat. Sci. 42(11): 1755–1765.
- Bell, M. C. 1973. Fisheries handbook of engineering requirements and biological criteria. U.S. Army Corps of Engineers. Fish Passage Development and Evaluation Program, North Pacific Division, Portland, Ore.
- Bell, M. C. 1986. Fisheries handbook of engineering requirements and biological criteria. U.S. Army Corps of Engineers, Fish Passage Development and Evaluation Program, North Pacific Division, Portland, Ore.
- Bell, M. C. 1991. Fisheries handbook of engineering requirements and biological criteria. U.S. Army Corps of Engineers. Fish Passage Development and Evaluation Program, North Pacific Division, Portland, Ore.
- Beschta, R. L. 1997. Riparian shade and stream temperature: An alternative perspective. Rangelands 19: 25–28.
- Beschta, R. L., R. E. Bilby, G. W. Brown, L. B. Holtby, and T. D. Hofstra. 1987. Stream temperature and aquatic habitat: Fisheries and forestry interactions. In E. O. Salo and T. W. Cundy (eds.), Streamside management: Forestry and fisheries interactions. College of Forest Resources, University of Washington, Seattle. Contribution number 57. Proceedings of a Symposium held at the University of Washington, 12–14 February 1986. p. 191–231

- Bisson, P. A. and G.E. Davis. 1976. Production of juvenile chinook salmon, *Oncorhynchus tshawytscha*, in a heated model stream. NOAA Fish. Bull. 74: 763-774.
- Black, M. C., D. S. Millsap, and J. F. McCarthy. 1991. Effects of acute temperature change on respiration and toxicant uptake by rainbow trout, *Salmo gairdneri* (Richardson). Physiol. 64(1): 145-168.
- Brett, J. R. 1952. Temperature tolerance in young Pacific Salmon, genus *Oncorhynchus*. J. Fish. Res. Bd. Can. 9(6): 265-323.
- Brett, J. R., M. Hollands, and D. F. Alderdice. 1958. The effect of temperature on the cruising speed of young sockeye and coho salmon. J. Fish. Res. Bd. Can. 15(4): 587-605.
- Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. 11(1): 99-113.
- Brett, R. J., W. C. Clarke, and J. E. Shelbourn. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile chinook salmon *Oncorhynchus tshawytscha*. Can. Tech. Rep. Fish. Aquat. Sci. No. 1127.
- Bumgarner, J., G. Mendel, D. Milks, L. Ross, M. Varney, and J. Dedloff. 1997. Tucannon River spring chinook hatchery evaluation. 1996 Annual report. Washington Department of Fish and Wildlife, Hatcheries Program Assessment and Development Division. Report #H97-07. Produced for U.S. Fish and Wildlife Service. Cooperative Agreement 14-48-000196539.
- Burrows, R. 1963. Water temperature requirements for maximum productivity of salmon. In Water temperature influences, effects, and control. Proc. 12th Northwest Symp. Water Pollution Research. U.S. Department of Health, Education, and Welfare, Public Health Service, Pacific Northwest Water Laboratory, Corvallis, Ore. p. 29-38.
- Chao, Y., M. Ghil, and J. McWilliams. 2000. Pacific interdecadal variability in this century's sea surface temperatures. Geophys. Res. Ltrs. 27: 2261.
- Chapman, D., A. Giorgi, M. Hill, A. Maule, S. McCutcheon, D. Park, W. Platts, K. Pratt, J. Seeb, L. Seeb, and F. Utter. 1991. Status of Snake River chinook salmon. Report to Pacific Northwest Utilities Conference Committee, Portland, Ore. 531 p.
- Clarke, W. C., and J. E. Shelbourn. 1985. Growth and development of seawater adaptability by juvenile fall chinook salmon (*Oncorhynchus tshawytscha*) in relation to temperature. Aquaculture 45: 21-31.

- Colgrove, D. J., and J. W. Wood. 1966. Occurrence and control of *Chondrococcus columnaris* as related to Fraser River sockeye salmon. IPSFC Progress report no. 15. Int. Pac. Salmon Fish. Comm., Vancouver, B.C., Canada. 51 p.
- Countant, C. C. 1977. Compilation of temperature preference data. J. Fish Res. Bd. Can. 34: 739–745.
- DeHart, D.A. 1975. Resistance of three freshwater fishes to fluctuating thermal environments. M.S. Thesis, Oregon State University, Corvallis.
- Dauble, D. D., and R. P. Mueller. 1993. Factors affecting the survival of upstream migrant adult salmonids in the Columbia River basin. Recovery issues for threatened and endangered Snake River salmon. Technical Report 9 of 11. Prepared for the U.S. Department of Energy, Bonneville Power Administration, Div. Fish Wildl., Project No. 98-026, Portland, Ore., June 1993.
- Dong, J. N. 1981. Thermal tolerance and rate of development of coho salmon embryos. M.S. thesis, University of Washington, Seattle.
- Donaldson, J. R. 1955. Experimental studies on the survival of the early stages of chinook salmon after varying exposures to upper lethal temperatures. M.S. thesis, University of Washington, Seattle.
- Dunham, J., J. Lockwood, and C. Mebane. 2001. Issue Paper 2. Salmonid distributions and temperature. Prepared as Part of Region 10 Temperature Water Quality Criteria Guidance Development Project. EPA-910-D-01-002. Available at <http://yosemite.epa.gov/R10/WATER.NSF/1507773cf7ca99a7882569ed007349b5/ce95a3704aeb5715882568c400784499?OpenDocument>
- Eaton, J. G., J. H. McCormick, B. E. Goodno, D. G. O'Brian, H. G. Stefany, M. Hondzo, and R. M. Scheller. 1995. A field information-based system for estimating fish temperature tolerances. Fisheries 20(4): 10–18.
- Ebersol, J. L. 2002. Heterogeneous thermal habitat for Northeast Oregon stream fishes. Ph.D. Thesis, Oregon State University, Corvallis. 201 p.
- Elliott, J. M., 1981. Some aspects of thermal stress on freshwater teleosts. In A. D. Pickering (ed.), Stress and fish. Academic Press, London. p. 209–245.
- Environmental Protection Agency (EPA). 1985. Ambient Water Quality Criteria for Ammonia, (EPA 440/5-85-001).
- Environmental Protection Agency (EPA). 2001. Draft EPA Region 10 guidance for state and tribal temperature water quality standards. U.S. EPA, Seattle, Wash. 33 p.

- Environmental Protection Agency (EPA) and National Marine Fisheries Service (NMFS). 1971. Columbia River Thermal Effects Study. Volume 1. Biological Effects Study. U.S. Environmental Protection Agency and National Marine Fisheries Service, Seattle, Wash. 102 p.
- Everson, L. B. 1973. Growth and food consumption of juvenile coho salmon exposed to natural and elevated fluctuating temperatures. M.S. Thesis, Oregon State University, Corvallis. 68 p.
- Ferguson, R. G. 1958. The preferred temperatures of fish and their midsummer distribution in temperature lakes and streams. J. Fish. Res. Bd. Can. 15: 607–624.
- Fish, F. F., and M. G. Hanavan. 1948. A report upon the Grand Coulee fish-maintenance project 1939–1947. Special Science Report 55, U.S. Fish and Wildlife Service, Washington, D.C. 63 p.
- Flett, P. A., K. R. Munkittrich, G. Van Der Kraak, and J. F. Leatherland. 1996. Overripening as the cause of low survival to hatch in Lake Erie coho salmon (*Oncorhynchus kisutch*) embryos. Can. J. Zool. 74: 851–857.
- Fryer, J. L., and Pilcher K. S. 1974. Effects of temperature on diseases of salmonid fishes. U.S. Environmental Protection Agency, Office of Research and Development. Ecological Research Series. EPA-660/3-73-020. 114 p.
- Garling, D. L., and Masterson M. 1985. Survival of Lake Michigan chinook salmon eggs and fry incubated at three temperatures. Prog. Fish-Culturalist. 47: 63–66.
- Groberg, W. J. Jr., R. H. McCoy, K. S. Pilcher, and J. L. Fryer. 1978. Relation of water temperature to infections of coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytsch*), and steelhead trout (*Salmo gairdneri*) with *Aeromonas salmonicida* and *A. hydrophila*. J. Fish Res. Bd. Can. 35: 1–7.
- Groberg, W. J. Jr., J. S. Rohavec, and J. L. Fryer. 1983. The effects of water temperature on infection and antibody formation induced by *Vibrio anguillarum* in juvenile coho salmon (*Oncorhynchus kisutch*). J. World Maricul. Soc. 14: 240–248.
- Groot, C., and L. Margolis, eds. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver. 564 p.
- Hallock, R. J., Elwell R. F., Fry D. H. 1970. Migrations of adult kind salmon *Oncorhynchus tshawytscha* in the San Joaquin delta as demonstrated by the use of sonic tags. Calif. Dept. Fish. Game. Fish. Bull. 151. 92 p.
- Heath, A. G., and G. M. Hughes. 1973. Cardiovascular and respiratory changes during heat stress in rainbow trout (*Salmo gairdneri*). J. Exp. Biol. 59: 323–338.

- Heming, T. A. 1982. Effects of temperature on utilization of yolk by chinook salmon (*Oncorhynchus tshawytscha*) eggs and alevins. *Can. J. Fish. Aquat. Sci.* 39: 184–190.
- Heming, T. A., J. E. McInernery, and D. F. Alderdice. 1982. Effect of temperature on initial feeding in alevins of chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 39(12): 1554–1562.
- Hicks, M. 2000. Evaluating standards for protecting aquatic life in Washington's surface water quality standards. Draft discussion paper and literature summary. Washington State Department of Ecology, Olympia, Wash.
- Hoar, W. S. 1988. The physiology of smolting salmonids. *In* W. W. Hoar and D. J. Randall (eds.), *Fish physiology*, Vol. XIB. Academic Press, New York. p. 275–343.
- Hokanson, K. E. F., C. F. Kleiner, and T. W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. *J. Fish. Res. Bd. Can.* 34: 639–648.
- Howe, G.E., L. L. Marking, T. D. Bills, J. J. Rach, and F. L. Mayer Jr. 1994. Effects of water temperature and pH on toxicity of terbufos, trichlorfon, 4-nitrophenol, and 2,4-dinitrophenol to the amphipod *Gammarus pseudolimnaeus* and rainbow trout (*Oncorhynchus mykiss*). EPA/600/J-94/125. *Environ. Toxicol. Chem.* 13(1): 51–66.
- Idler, D. R., and W. A. Clemens. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart Lakes. IPSFC Prog. Rep., Int. Pac. Salmon Fish. Comm., Vancouver, B.C., Canada. 80 p.
- Independent Science Group. 1996. Return to the River Report. Document number 96-6, Northwest Power Planning Council Independent Scientific Advisory Board, Portland, Ore.
- Jobling, M. 1981. Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. *J. Fish Biol.* 19: 439–455.
- Jobling, M. 1994. *Fish bioenergetics*. Chapman & Hall, London. 309 p.
- Konecki, J. T., C. A. Woody, and T. P. Quinn. 1995. Critical thermal maxima of coho salmon (*O. kitsuch*) under field and lab acclimation regimes. *Can. J. Zool.* 73: 993–996.
- MacLeod, J. C., and E. Pessah. 1973. Temperature effects on mercury accumulation, toxicity, and metabolic rate in rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Bd. Can.* 30: 485–492.
- Marine, K. R. 1997. Effects of elevated water temperature on some aspects of the physiological and ecological performance of juvenile chinook salmon (*Oncorhynchus tshawytscha*):

- Implications for management of California's Central Valley salmon stocks. M.S. thesis, University of California, Davis. 71 p.
- Marine, K. R., and J. J. Cech Jr. 1998. Effects of elevated water temperature on some aspects of the physiological and ecological performance of juvenile chinook salmon (*Oncorhynchus tshawytscha*): Implications for management of California's chinook salmon stocks. Stream temperature monitoring and assessment workshop. 12–14 January 1998. Sacramento, California. Forest Science Project, Humboldt State University, Arcata, California.
- Materna, E. 2001. Issue Paper 4. Temperature interaction. Prepared as part of U.S. EPA Region 10 Temperature Water Quality Criteria Guidance Development Project. EPA-910-D-01-004. Available at <http://yosemite.epa.gov/R10/WATER.NSF/1507773cf7ca99a7882569ed007349b5/ce95a3704aeb5715882568c400784499?OpenDocument>
- Mayer, F. L. Jr., L. L. Marking, T. D. Bills, and G. E. Howe. 1994. Physiochemical factors affecting toxicity in freshwater: Hardness, pH, and temperature. *In* J. L. Hamelink, P. F. Landrum, H. L. Bergman, and W. H. Benson (eds.), Bioavailability: Physical, chemical, and biological interactions. CRC Press, Boca Raton, Fla. p. 5–22. EPA/600/A-94/199.
- McCullough, D. A. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids, with special reference to chinook salmon. Water Resource Assessment, U.S. EPA 910-R-99-010, Columbia River Inter-Tribal Fish Commission, Portland, Ore. 291 p.
- McCullough, D., S. Spalding, D. Sturdevant, M. Hicks. 2001. Issue Paper 5. Summary of technical literature examining the physiological effects of temperature on salmonids. Prepared as part of U.S. EPA Region 10 Temperature Water Quality Criteria Guidance Development Project. EPA-910-D-01-005. Available at <http://yosemite.epa.gov/R10/WATER.NSF/1507773cf7ca99a7882569ed007349b5/ce95a3704aeb5715882568c400784499?OpenDocument>
- McGeer, J.C., L. Baranyi, and G.K. Iwama. 1991. Physiological responses to challenge tests in six stocks of coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 48: 1761–1771.
- Murray, C. B., and T. D. Beacham. 1986. Effect of varying temperature regimes on the development of pink salmon (*Oncorhynchus gorbuscha*) eggs and alevins. *Can. J. Zool.* 64: 670–676.
- Murray, C. B., and J. D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. *Can. J. Zool.* 66(1): 266–273.

- Nielsen, J. L., T. E. Lisle, and V. Ozaki. 1994. Thermally stratified pools and their use by steelhead in Northern California streams. *Trans. Am. Fish. Soc.* 123: 613–626.
- Olson, P. A., and R. F. Foster. 1955. Temperature tolerance of eggs and young of Columbia River chinook salmon. *Trans. Am. Fish. Soc.* 85: 203–207.
- Ordal, E. J., and R. E. Pacha. 1963. The effects of temperature on disease in fish. *Proceedings of the Twelfth Pacific Northwest Symposium on Water Pollution Research*. U.S. Department of the Interior, Federal Water Pollution Control Administration, Northwest Region, Corvallis, Ore. p. 39–56.
- Oregon Department of Environmental Quality (ODEQ). 1995. Water quality standards review. Standards and Assessment Section, ODEQ, Portland, Ore.
- Orsi, J. J. 1971. Thermal shock and upper lethal temperature tolerances of young king salmon, *Oncorhynchus tshawytscha*, from the Sacramento-San Joaquin River system. Anadromous Fisheries Branch Administrative Report No. 71-11. California Department of Fish and Game, Sacramento, Calif. 16 p.
- Paladino, F. V., J. R. Spotila, J. P. Schubauer, and K. T. Kowalski. 1980. The critical thermal maximum: A technique used to elucidate physiological stress and adaptation in fishes. *Rev. Can. Biol.* 39(2): 115–122.
- Pacific Northwest Salmon Habitat Indicators Work Group (PNWSHIWG). 1998. Toward “A Small but Powerful” set of regional salmon habitat indicators for the Pacific Northwest. Prepared for the PNWSHIWG by the Green Mountain Institute for Environmental Democracy, Montpelier, Vermont.
- Poole, G. C., and C. H. Berman. 2001. An ecological perspective on in-stream temperature: Natural heat dynamics and mechanisms of human-caused thermal degradation. *Environ. Manage.* 27(6): 787–802.
- Poole, G., J. Dunham, M. Hicks, D. Keenan, J. Lockwood, E. Materna, D. McCullough, C. Mebane, J. Risley, S. Sauter, S. Spalding, and S. Sturdevant. 2001a. Scientific issues relating to temperature criteria for salmon, trout, and char native to the Pacific Northwest. A summary report submitted to the policy workgroup of the U.S. EPA Region 10 Water Temperature Criteria Guidance Project. EPA 910-R-01-007. Available at <http://yosemite.epa.gov/R10/WATER.NSF/1507773cf7ca99a7882569ed007349b5/ce95a3704aeb5715882568c400784499?OpenDocument>
- Poole G., J. Risley, and M. Hicks. 2001b. Issue Paper 3. Spatial and temporal patterns of stream temperature (revised). Prepared as part of U.S. EPA Region 10 Temperature Water quality Criteria Guidance Development Project. EPA-910-D-01-003. Available at <http://yosemite.epa.gov/R10/WATER.NSF/1507773cf7ca99a7882569ed007349b5/ce95a3704aeb5715882568c400784499?OpenDocument>

- Raleigh R. F., W. F. Miller, and P. C. Nelson. 1986. Habitat suitability index models and instream flow suitability curves: Chinook salmon. U.S. Fish Wildlf. Serv. Biol. Rep. 82(10.122). 64 p.
- Redding, J. M., and C. B. Schreck. 1979. Possible adaptive significance of certain enzyme polymorphisms in steelhead trout (*Salmo gairdneri*). J. Fish. Res. Bd. Can. 36: 544–551.
- Reiser, D. W., and T. C. Bjorn. 1979. Habitat requirements of anadromous salmonids. Gen. Tech. Rep. PNW-96. USDA Forest Service. Pacific Northwest Forest and Range Experiment Station, Portland, Ore. 54 p.
- Reutter, J. M., and C. E. Herdendorf. 1974. Laboratory estimates of the seasonal final temperature preferenda of some Lake Erie fish. Proc. 17th Conf. Great Lakes Res. 1974: 59–67.
- Rombough, P. J. 1988. Growth, aerobic metabolism, and dissolved oxygen requirements of embryos and alevins of steelhead, *Salmo gairdneri*. Can. J. Zool. 66: 651–660.
- Roper, B. B., D. L. Scarnecchia, T. J. L. Marr. 1994. Summer distribution of and habitat use by chinook salmon and steelhead within a major basin of the South Umpqua River, Oregon. Trans. Am. Fish. Soc. 123: 298–308.
- Sandercock, F. K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). In C. Groot and L. Margolis (eds.), Pacific salmon life histories. University of British Columbia Press, Vancouver. p. 395–445.
- Sauter, S. T. 1996. Thermal preference of spring and fall chinook salmon during smoltification. M.S. thesis. Portland State University, Portland, Ore.
- Sauter, S. T., J. McMillan, and J. Dunham. 2001. Issue Paper 1. Salmonid behavior and water temperature. Prepared as part of U.S. EPA Region 10 Temperature Water Quality Criteria Guidance Development Project. EPA-910-D-01-001. Available at <http://yosemite.epa.gov/R10/WATER.NSF/1507773cf7ca99a7882569ed007349b5/ce95a3704aeb5715882568c400784499?OpenDocument>
- Sedell, J. R., and J. L. Froggatt. 1984. Importance of streamside forests to large rivers: The isolation of the Willamette River, Oregon, USA, from its floodplain by snagging and streamside forest removal. Int. Ver. Theoret. Angew. Limnol. Verhandl 22: 1828–1834.
- Seymour, A. H. 1956. Effects of temperature upon young chinook salmon. Ph.D. thesis, University of Washington, Seattle. 127 p.
- Spigarelli, S. A. 1975 Behavioral responses of Lake Michigan fishes to a nuclear power plant discharge. In Environmental effects of cooling systems in nuclear power plants. International Atomic Energy Agency (IAEA), Vienna. p. 479–498.

- Stabler, D. F. 1981. Effects of altered flow regimes, temperatures, and river impoundment on adult steelhead trout and chinook salmon. M.S. thesis, University of Idaho, Moscow. 84 p.
- Sullivan, K., D. J. Martin, R. D. Carwell, J. E. Toll, and S. Duke. 2000. An analysis of the effects of temperature on salmonids of the Pacific Northwest with implications for selecting temperature criteria. Sustainable Ecosystems Institute, Portland, Ore.
- Tang J., Bryant M.D., Brannon E. L. 1987. Effect of temperature extremes on the mortality and development rates of coho salmon embryos and alevins. *Prog. Fish-Cult.* 49(3): 167–174.
- Velsen, F. P. J. 1987. Temperature and incubation of Pacific salmon and rainbow trout. Compilation of data on median hatching time, mortality, and embryonic staging. Canadian Data Report of Fisheries and Aquatic Sciences 626.
- Washington Department of Ecology (WDOE). 1999. Evaluating standards for protecting aquatic life in Washington's surface water quality standards. Temperature criteria. Preliminary review draft discussion paper. Draft report and appendices. WDOE, Olympia, Wash.
- Williams, I. V., U. H. M. Fagerlund, J. R. McBride, G. A. Strasdine, H. Tsuyuki, and E. J. Ordal. 1977. Investigation of prespawning mortality of 1973 Horsefly River sockeye salmon. IPSFC Progress report no. 37. Int. Pac. Salmon Fish. Comm., Vancouver, B.C., Canada. 51 p.
- Wilson, W. J., M. D. Kelley, and P. R. Meyer. 1987. Instream temperature modeling and fish impact assessment for a proposed large-scale Alaska hydro-electric project. *In* J. F. Craig and J. B. Kemper (eds.), *Regulated streams*. Plenum Press, New York. p. 183–206.
- Wurtsbaugh, W. A., and G. E. Davis. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri*, Richardson. *J. Fish. Biol.* 11: 87–98.
- Zaugg, W. S. 1981. Relationships between smolt indices and migration in controlled and natural environments. *In* E. L. Brannon and E. O. Salo (eds). *Proceedings of the salmon and trout migratory behavior symposium*. School of Fisheries, University of Washington, Seattle. p. 173–183.
- Zaugg, W. S., and L. R. McLain. 1976. Influence of water temperature on gill sodium, potassium-stimulated ATPase activity in juvenile coho salmon (*Oncorhynchus kisutch*). *Comp. Biochem. Physiol.* 54A: 419–421.
- Zaugg, W. S., and H. H. Wagner. 1973. Gill ATPase activity related to parr-smolt transformation and migration in steelhead trout (*Salmo gairdneri*): Influence of photoperiod and temperature. *Comp. Biochem. Physiol.* 45B: 955–965.
- Zinichev, V. V., and A. I. Zotin. 1987. Selected temperature and optimums for development in prolarvae and larvae of chum salmon, *Oncorhynchus keta*. *J. Ichthyol.* 27(6): 141–144.